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THE ORIGIN AND NATURE OF THE EAR OF MAIZE
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OF ALL THE New World plants which excited the curiosity and wonder of the herbalists of the immediate post-Columbian period, none, perhaps, proved to be more intriguing than Indian corn or maize. The ears of this plant, and to a lesser extent the tassels, were quite baffling to the students of that period and have continued to perplex botanists for more than four centuries. Nowhere has the recognition of the peculiarities of the maize inflorescence been more vividly expressed than by Lyte in his *New Herbal* of 1619 (6)*. The page on which maize is described is reproduced as Plate VII of this paper. The description of the inflorescences is as follows: "This Corne is a marvellous strange plant, nothing resembling any other kind of grayne; for it bringeth forth his seede cleane contrarie from the place whereas the Floures grow, which is against the nature and kinds of all other plants, which bring forth their fruit there, whereas they have borne their Floure. . . . at the highest of the stalkes, grow idle and barren eares, which bring forth nothing but the floures or blossomes. . . . "

The wonderment of the herbalist of the sixteenth cen-

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*This description, in slightly different form, first appeared in an edition entitled *A Nievve Herball* in 1578.

tury has persisted almost undiminished to the botanist of the twentieth. True, the modern student recognizes that Lyte's description of maize is somewhat lacking in accuracy from the technical botanical standpoint. Maize does not, as Lyte believed, bear its seeds "cleane contrarie from the place whereas the Floures grow" and therefore it is not, as he contended, "against the nature and kinds of all other plants." Nevertheless, the botanist of today would not deny that maize is indeed a "marvellous strange plant," and he would unhesitatingly agree with Lyte that its uniqueness lies in its inflorescences, particularly in the pistillate inflorescence, the ear.

In its general vegetative characteristics maize does not differ essentially from other grasses especially the larger cultivated species; its affinity to sugar cane and the sorghums, for example, is easily recognized. But nowhere among the Gramineae, indeed nowhere in the Plant Kingdom, is there a fruit which in its external aspects at least seems to be more than remotely comparable to the ear of maize. It is quite understandable, therefore, that the ear of maize has been the subject of numerous observations, investigations and conjectures. Nor is it surprising that the problem of its origin and morphological nature has remained to a large extent unsolved.

This paper, despite the unqualified language of its title, does not presume to present a final solution to the problem of the origin and nature of the ear of maize. Botanical problems of this kind are seldom susceptible of complete and definitive solutions. However, in the course of extensive studies of maize-teosinte hybrids and of hybrids of pod corn with a peculiar variety of maize obtained from the Guarany Indians of Paraguay, a number of interesting phenomena have been encountered which appear to shed new light upon the problem of the maize ear. Before considering the new facts, it seems de-

sirable to review the previous evidence and hypotheses which bear upon the problem. Only the essential features of the earlier hypotheses will be considered here since the rather extensive literature on the subject has been thoroughly reviewed in recent years by several writers. The reader is referred to the papers of Weatherwax (19), Mangelsdorf and Reeves (13), and Reeves (15) for additional details.

Historical Considerations

The Maize Ear Described

The ear of maize, though not easily interpreted, is not difficult to describe. It is a spike upon whose thickened axis (the cob) naked grains (caryopses) are borne in longitudinal or somewhat spiral rows; eight, ten, twelve or more in number. The number of rows is always even because the spikelets upon which the grains are borne are paired, a characteristic in which maize differs from its nearest relatives, teosinte and Tripsacum, whose spikelets are solitary. Each rank of paired spikelets is clearly the equivalent of two rows of grain in the mature ear. The ear is enclosed in husks which are modified, overlapping leaf-sheaths. The ear is obviously the terminal inflorescence of a lateral branch whose internodes have, probably during the course of domestication, become drastically contracted.

Homology of Ear and Tassel

The general nature of the ear is sufficiently clear so that there can be little doubt that it is the homologue of the central spike* of the staminate inflorescence, the tassel. This homology may have been vaguely suspected by some of the earlier students including Wigand, Ascher-

* In one of his recent papers Weatherwax (19) calls this structure a "terminal raceme." I prefer the older but equally appropriate "central spike."

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son and Goebel,* but it seems to have been first clearly recognized by Mrs. Kellerman (9) who postulated that the ear has developed phylogenetically from the *central stem‡* of the primitive tassel. Montgomery (14) apparently unaware of Mrs. Kellerman's suggestion, independently arrived at the same conclusion, illustrating it with an interesting series of transition stages to show how the change from a staminate central spike of the tassel to a pistillate ear might have occurred.

Since the appearance of Montgomery's paper the homology of the ear with the central spike of the tassel has not been seriously challenged except, perhaps, by indirection. Strong evidence, amounting almost to proof, of the homology of the two structures has recently been furnished by Langham (11) who showed that in segregates of maize-teosinte hybrids there is a close correlation between the ear and the central spike of the tassel in the expression of distichy and polystichy. A recent paper by Bonnett (3) is illustrated with striking photographs which reveal, among other things, that in the early stages of development the two structures, ear and central spike, are scarcely distinguishable.

Anderson (1) has recently pointed out that some of the important characteristics of the ear are closely correlated with characteristics of the lateral branches of the tassel. These observations, as will be shown later, are not in conflict with the conception of the ear as the homologue of the central spike of the tassel.

The fact that the ear is the homologue of the central spike does not, however, solve the problem of the origin of the ear. As Collins (4) pointed out many years ago,

* Cf. Weatherwax (19) or Mangelsdorf and Reeves (13) for references.

‡ Italics hers.

the central spike is as much in need of explanation as the ear.

Hypotheses Regarding the Ear of Maize

There have been three general hypotheses regarding the ear of maize : (1) That it is the product of the fusion of two or more distichous (two-ranked) spikes. (2) That it originated from the shortening and twisting of a distichous spike. (3) That it is the result of the transformation of a panicle to a spike through the reduction of branches.

The Fusion Hypothesis. It is not surprising that botanists familiar with the compound nature of many fruits should, when confronted with an ear of maize, think immediately in terms of fusion. And when branched ears, ears apparently "disrupted" into their component parts, are encountered, the fusion hypothesis becomes almost inevitable. Little wonder that this hypothesis is the oldest of the three and has been, by all odds, the most popular. Ascherson, Hackel, Harshberger, Gernert, Wordsell, and Goebel* have all interpreted the ear of maize as arising through the fusion of two-ranked spikes either like those of teosinte or Tripsacum, or like the lateral branches of the maize tassel.

The serious weakness of the fusion hypothesis, so far as maize is concerned, is that there is no concrete evidence in support of it and considerable evidence in conflict with it. Branched ears, bifurcated or many-branched at the tip or bearing branches at the base, have repeatedly been regarded as evidence for the compound nature of the maize ear. But the majority of these branched ears prove upon examination to represent a type of branching which

*Cf. Weatherwax (19) or Mangelsdorf and Reeves (13) for references.

is not easily attributable to the "disruption" of a compound structure into its component parts. Weatherwax (16) regards ears branched at the tip as nothing more than anomalies "giving no more clue to the past than is afforded by Siamese twins." And now Reeves (15) has virtually committed to the category of *reductio ad absurdum* the argument for fusion based upon branching, when he points out that the two types of branching most commonly encountered in the ear, basal branching and bifurcation of the tip, have their counterparts in the stem, the first in the well-known basal tillering or "suckering" of the stalk, the second in the bifurcated stalks which he described (15). Reeves contends that if branching of the ear is regarded as evidence of its compound nature, then corresponding types of branching in the culm must be regarded as evidence that it, too, is a compound structure resulting from fusion.

Aside from branched ears, which upon close examination obviously fail to support the fusion hypothesis, what is the evidence for fusion? Apparently there is none. Weatherwax (18) states that both the young ear and the young tassel develop from ordinary growing points and that there is nothing to suggest a compound nature. Bonnett's studies (3) support this statement, although he does not specifically discuss the question of fusion. Weatherwax has observed (19) that the vascular bundles of the cob are distributed in approximately the same manner as those of the stem and therefore furnish no indication of fusion. Reeves (15) too, has made a detailed study of the vascular system and the arrangement of the rachis segments and finds no structural feature of any kind which suggests that the maize ear is the product of fusion.

Weatherwax (16, 18, 19) seems to regard as the most critical evidence in conflict with the fusion theory, the

fact that the fusion of distichous branches (in which the spikelets are paired or must become paired to produce an ear of maize) should result in ears in which the number of ranks of paired spikelets is always even and the number of rows of grain is always a multiple of four. Thus a fusion of two such spikes or branches would produce an ear with four ranks of paired spikelets and eight rows of grain; a fusion of three spikes or branches, an ear with six ranks of paired spikelets and twelve rows of grain, etc. Weatherwax assumes that ears in which the number of ranks of paired spikelets is odd and the number of rows of grain not a multiple of four (ears with ten, fourteen and eighteen rows of grain, for example) cannot have been the product of fusion of two-ranked spikes. Since such ears do occur Weatherwax concludes that the fusion hypothesis is confronted with serious mathematical inconsistencies.

Kempton (10), in an attempt to reconcile these apparent inconsistencies, has suggested that ears in which the number of ranks of paired spikelets is odd may be the result of the abortion of a row of paired spikelets or the abortion of the pediceled* spikelets in both ranks of one of the component branches. Kempton was of the opinion that both of these phenomena are of common occurrence, but it is now doubtful if either one occurs. Weatherwax (19) found no vestiges of the supposedly aborted spikelets and Dr. Reeves and I have examined numerous ten-rowed ears without finding a trace of them, although there is no difficulty in seeing them in both teosinte and Tripsacum where normally only one spikelet in each pair is functional.

Kempton (10) also suggested that ears in which the

* Both members of a pair of pistillate spikelets are actually sessile, but one is potentially pediceled and is the homologue of the pediceled staminate spikelet.

number of rows of grain is a multiple of four are more numerous than ears in which the row number is not a multiple of four. Even before the suggestion was made, East (7) had shown that such is, indeed, the case. East offered no morphological explanation for the multimodal distribution and it still remains to be satisfactorily explained. Reeves (unpublished) has suggested that the peculiar distribution reported by East may be the result of past selection for straight-rowed ears, a suggestion based on the fact that there is a tendency, discovered by Fujita (8), for ears with an odd number of ranks of paired spikelets to be twisted.

But whatever the explanation of the low frequency of ears with ranks of paired spikelets in odd numbers, the fact that *any* ears of this kind occur has generally been regarded as evidence against the fusion theory. Perhaps more weight has been assigned to this evidence than is deserved. There are undoubtedly ways (one will be mentioned later) in which rows of spikelets might be lost without leaving readily discoverable vestiges. Furthermore if fusion is thought of in a phylogenetic rather than in an ontogenetic sense, it is scarcely necessary to assume that the compound structure resulting from fusion must still exhibit all of the features of its original component parts. Finally the absence of anatomical evidence of fusion is by no means final proof that it has not occurred. There are numerous structures in plants in which anatomical evidence for fusion is lacking or at least not readily discernible, but which are nevertheless regarded as compound structures. In these instances, however, some other kind of evidence for fusion is usually at hand; for example, a series of forms involving different species which illustrates a transition from the condition in which the components are entirely separated to that in which they are completely joined. In the case of maize there

appears to be no evidence *of any kind* to support the fusion hypothesis with respect to the ear. Yet fusion does occur in maize. It is almost certain that the slightly branched styles, the well-known "silks" are compound structures resulting from the fusion of the two stylar branches characteristic of grasses.* I have seen several cases of fusion of the pedicel of a staminate spikelet with the surface of the rachis. And an actual instance of the fusion of two of the branches of a maize tassel, the kind of fusion which might have given rise to the ear, will be described later in this paper. Nevertheless, the fusion hypothesis of the origin of the maize ear, though the most obvious, and at first glance the most plausible, actually appears to have little to commend it.

Reduction of Branches. The second hypothesis, that the ear of maize has been derived from a panicle through the reduction of branches until each branch is now represented by a pair of spikelets, was suggested by Collins (4). But the general theory that spikes are more specialized than panicles and have originated from these through the reduction of branches is, as Reeves (15) has pointed out, an old one.

This hypothesis would seem to be especially appropriate when applied to maize whose staminate inflorescence, the tassel, is a perfect illustration of a combination of spike and panicle, a structure in which the reduction of branches either has not proceeded to completion or has been confined to the upper part of the inflorescence. Furthermore it is not difficult to find extreme forms which lend credence to the hypothesis; for example, tassels which consist only of central spikes or ears which bear well-defined basal branches.

Collins felt that the chief objection to this hypothesis

*Cf. Weatherwax (18) p. 123.

lay in the fact that in most cases the change from branches to spikelet is abrupt. In the tassel there are usually only well-defined branches at the base and only spikelets on the central spike. In most cases there is no transition from branches to spikelets. Collins found some evidence of such a transition in varieties of pod corn, but the condition in pod corn was by no means as convincing as the various transition stages later described and illustrated by Weatherwax (16) in branch (ramosa) maize.

The studies of Bonnett (3) have a bearing on this problem for they show that in the development of the tassel there are no discernible differences between the initials that become the lateral branches and those which become differentiated into spikelets.

The conception of the ear of maize as a spike homologous to the central spike of the tassel, and like the latter having arisen through the reduction of branches, (a reduction usually completed in the ear, but seldom in the tassel) appears to be clear, reasonable and in complete harmony with the facts. Weatherwax (16, 19) contends, however, that this hypothesis alone is not adequate since it does not answer the question of how the polystichous condition originated in maize or other grasses. He, therefore, interprets the maize ear in terms of spiral phyllotaxy. The four-rowed ear (like the arrangement of the leaves on the stem) is regarded as including a single spiral; the eight-rowed ear includes two spirals, etc.

Weatherwax has made an important contribution in recognizing and describing the spiral phyllotaxy characteristics of some (probably not of all) maize ears, and in showing the resemblance of the maize ear to the spikes of other grasses such as Pennisetum. Phyllotaxy, however, describes rather than explains the change from the distichous condition typical of the grasses in general to the polystichous condition characteristic of the inflores-

cences of maize. To say that the many-ranked ear of maize departs from its two-ranked prototype by virtue of its more complex phyllotaxy is scarcely more explanatory than to say that the former has more numerous ranks than the latter. Nevertheless phyllotaxy, as will become apparent later, is immensely important.

Actually, as Reeves (15) points out, the polystichous inflorescence is sufficiently common in various genera of grasses so that no special explanation of its occurrence in maize is required. Its origin is a problem of the Gramineae as a group rather than of maize alone. The uniqueness of maize lies not so much in its polystichous ear as in the fact that its staminate inflorescence is usually a modified panicle while its pistillate inflorescence is usually a spike. Collins' hypothesis furnishes a very satisfactory explanation of the steps involved in the transformation of one to the other.

Anderson's (1) observations, previously mentioned, that the characteristics of the ear are correlated with characteristics of the lateral branches of the tassel, may be interpreted to mean, not that the ear is the product of fusion and that the lateral branches are homologues of its component parts, but simply that the lateral branches are capable of revealing what kind of panicle it is that has become modified to produce the ear.

Twisting of a Two-Ranked Spike. The third hypothesis, that the polystichous maize ear arose through the shortening and twisting of a two-ranked spike, such as the spike of teosinte, was also formulated by Collins (5). This hypothesis grew out of observations made by him on the pistillate spikes of an F_2 population of a maize-teosinte hybrid from which a series of specimens could be selected to illustrate the steps involved in changing a structure like the spike of teosinte to one resem-

bling the ear of maize. These steps, not necessarily in this order, are as follows:

1. The solitary pistillate spikelets characteristic of teosinte become paired spikelets typical of maize as the aborted member of each pair becomes functional.

2. The axis of the rachis shortens with the result that adjacent rachis segments assume positions in the same horizontal plane and become "yoked" in pairs. This change, combined with the preceding one, results in a four-rowed ear.

3. A twisting of the axis causes alternate segments to assume positions in a plane at right angles to that occupied by adjacent segments above and below. This, combined with the changes already described, produces an eight-rowed ear. Ears with higher row numbers are produced by further twisting of the axis.

There is no doubt that the series of transition forms which Collins described do occur in segregates of maize-teosinte hybrids. Nor is there any doubt that the ear of maize *could* have arisen from the spike of teosinte through such a series of changes. Indeed if maize had originated from teosinte the changes which have actually occurred must have been very similar to those which Collins has described.

Collins did not imply, however, that maize had actually been derived from teosinte by this series of steps and in fact he carefully pointed out that these intermediate steps explained the evolution of the ear only in a mechanical sense.

Even in a strictly mechanical sense, however, the hypothesis has not been satisfactory. Weatherwax (19) has objected to it on the grounds that there is no evidence in maize of the supposed "yoking" of pairs of spikelets on opposite sides of the rachis. Collins believed that he had evidence for yoking in ears in which some of the rows

of grain were interrupted. He stated that among many ears examined, in which rows were dropped between the base and the tip of the ear, in no instance were the dropped rows either adjacent or separated by two rows, but always (when the dropped rows could be determined with reasonable certainty) on opposite sides of the ear.

Weatherwax (17) showed, however, that when rows are dropped between the base and tip of the ear, it is always a pair of adjoining rows which is eliminated and not rows on opposite sides of the rachis. It is difficult to see how Collins, usually a keen observer, could have been so completely in error in this instance. Actually his statement, though highly inaccurate, has some basis in fact; for in segregates of maize-teosinte hybrids there is in some four-ranked ears a definite tendency for the spikelets in one plane to be predominantly paired while those in the plane at right angles are predominantly single. In other words in ears in which yoking is obvious, there is a definite tendency for the spikelets diametrically opposed to each other on the axis to be alike with respect to the abortion and development of spikelets.

In considering the yoking hypothesis there is some danger, as has already been apparent in the case of the fusion hypothesis, of thinking only in rigid terms. Is it not possible that as the axis becomes thickened, the yoking, if it occurs at all, would become less obvious and the tendency for spikelets on opposite sides of the rachis to exhibit identical behavior would become less pronounced and would, indeed, disappear completely? Is it necessary, in other words, to conclude that yoking has not occurred in the development of the maize ear because the spikelets on opposite sides of the axis, in ordinary ears of maize, are not alike in their behvaior? These questions will be discussed further when new evidence from maize-teosinte hybrids is considered.

Evidence for Fusion

The fusion hypothesis, as has already been mentioned, has been, to a large extent, dismissed because (a) anatomical and other evidence for fusion has been lacking and (b) it has been thought that the hypothesis leads to mathematical inconsistencies with regard to row number. New evidence renders both of these objections somewhat less pertinent than they previously were.

During the summer of 1944, Mrs. P. C. Mangelsdorf in taking notes on the number of ranks in the central spike of tassels among segregates of maize-teosinte hybrids, encountered a clear-cut case of fusion of two of the lateral branches of the tassel. This is illustrated in Fig. 1. The two branches are joined for a distance of slightly more than half of their length. There is no doubt that this is a case of fusion rather than fasciation for the lower region in which the two parts are joined is distinctly four-ranked, a condition which I have never before encountered in a lateral branch of the tassel, while the two unjoined parts of the upper region are both distinctly two-ranked and differ in no important detail from the remaining branches on this tassel.

The fused portion of this branch is not radially symmetrical but exhibits a distinct dorsiventral character since only the adjoining edges of the two component parts are fused. Had the two entire dorsal surfaces of the branches become fused, or had a third branch become fused at both of its edges to the free edges of the other two, thus forming a cylinder, the structure would have been indistinguishable from the central spike of the tassel.

This single specimen makes it clear that a polystichous structure similar to the central spike of the tassel (which is the homologue of the ear) can arise in maize through

the fusion of distichous branches. It does not prove that the ear of maize did actually arise in this way, although it would undoubtedly have been regarded as proof by earlier proponents of the fusion hypothesis.

Also during the summer of 1944 my attention was called to some peculiarities of *Tripsacum dactyloides* (L.) L. by Dr. Leon Croizat who suggested that they seem to have a bearing on the question of fusion. In this species the inner surfaces of the several branches of the terminal inflorescences are so sculptured that the irregularities of one branch are reciprocal to those of the adjoining branch. Because of this the branches, when brought together, form a cylinder which bears spikelets on its circumference; a structure comparable to an ear of maize. I do not regard this condition as evidence for fusion as it is obviously nothing more than the result of the considerable compression to which the inflorescence is subjected while still in the sheath. The same condition in less conspicuous form is regularly encountered in maize tassels where the lateral

FIGURE 1. A case of fusion of two of the lateral branches of a maize tassel. The two-ranked branches are joined for slightly more than half of their length, but separated for the remainder.

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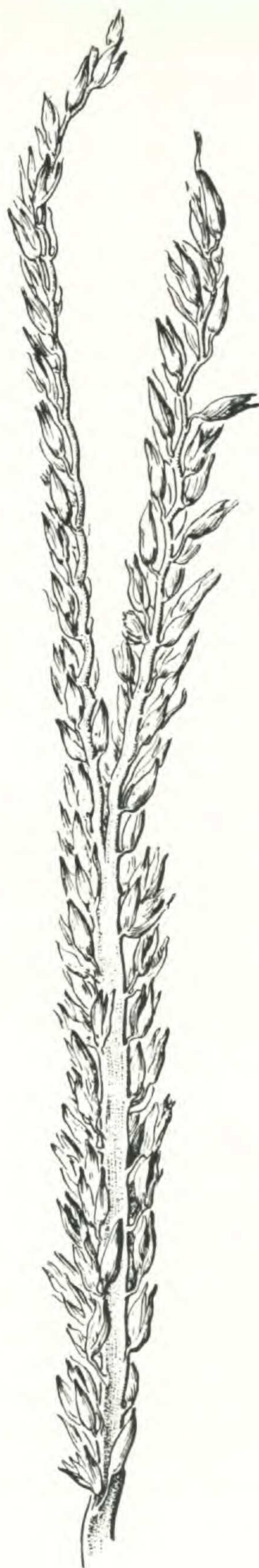
branches during development have been compressed around the central spike. Indeed compression is a common phenomenon in the grass inflorescence. Its importance has been clearly recognized by several students of the Gramineae and has been strongly emphasized by Arber (2). The Tripsacum inflorescence is of interest, in my opinion, not in indicating fusion, but in suggesting (as pointed out by Dr. Croizat) how maize ears with odd numbers of rows of paired spikelets and rows of grain not in multiples of four *might* have originated through fusion. This possibility is illustrated in Fig. 2. Fig. 2a
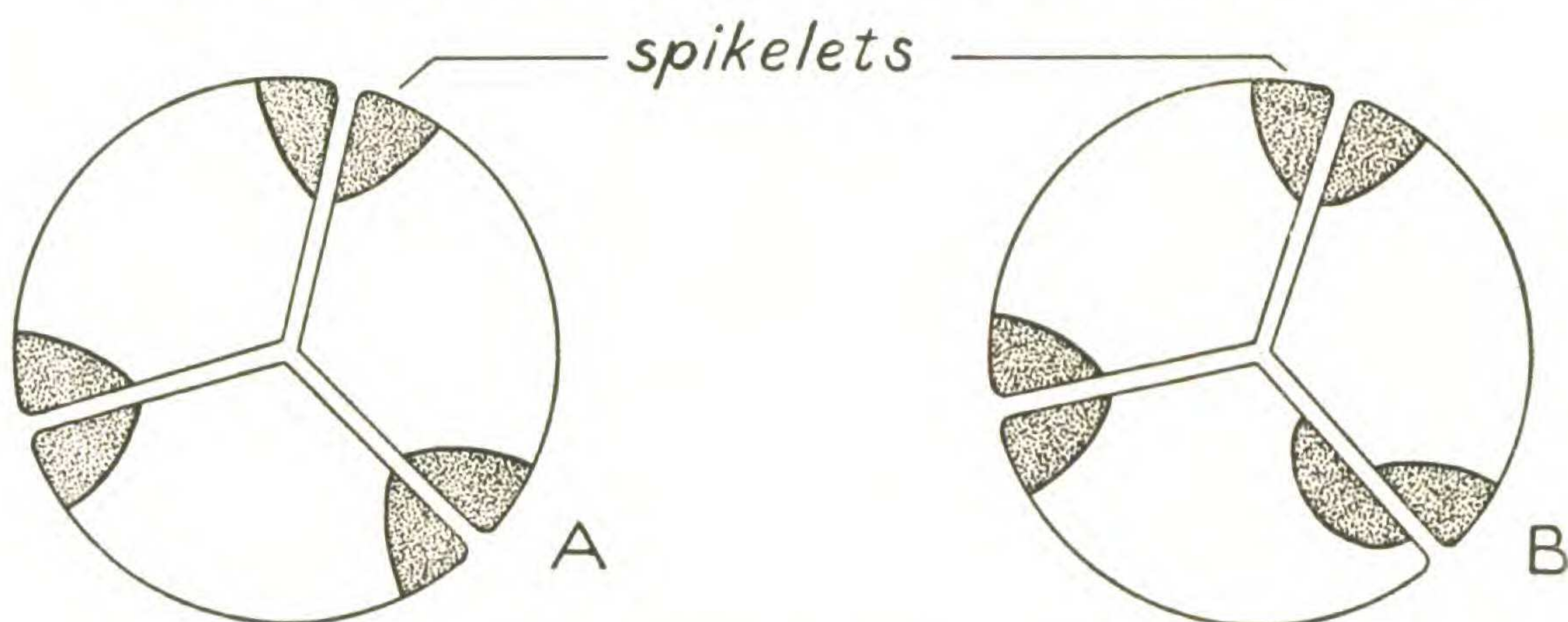

FIGURE 2. Diagrams showing how fusion of two-ranked branches such as those of Tripsacum might give rise to ears with rows of paired spikelets in odd numbers. With the development of the abortive spikelet, the structure illustrated in diagram A would give rise to a twelve-rowed ear. But the condition illustrated in B, because one row of spikelets is abnormally oriented and "buried," would produce a ten-rowed ear.

shows the condition most commonly encountered when three branches are brought together to form a cylinder. Had an ear of maize originated through the fusion of three branches such as these illustrated it would have become a twelve-rowed ear for the circumference of the axis bears six rows of spikelets which, though solitary in Tripsacum, are always paired in maize.

Fig. 2b illustrates a condition encountered much less

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commonly but by no means rarely. Here one of the branches is asymmetrical with respect to the position of its spikelets. Were these three branches to fuse to produce an "ear" it would be a ten-rowed ear for here the circumference bears only five rows of spikelets; the sixth is "buried" in the cob. Its vestiges, if they remain at all, are not likely to be found on the surface.

I do not intend to suggest that the ear of maize did actually originate from the fusion of two-ranked branches such as these of Tripsacum, nor do I wish to explain the occurrence of ears with rows of paired spikelets in odd numbers as the result of the "burying" of a row of spikelets in the cob. It is very doubtful if the points at which the spikelets are to appear are so rigidly fixed in the undifferentiated primordium of the spike that its accidental disorientation could result in the suppression of an entire row of spikelets. On the other hand, if this is true, then it is probably also true that ears with pairs of spikelets in odd numbers are not necessarily inconsistent with the fusion hypothesis. For if we think of fusion in rigid terms, the joining during ontogeny of spikes each bearing the primordia of two ranks of paired spikelets, then the condition illustrated in Fig. 2b is a reasonable and valid explanation of how a row of paired spikelets might be lost without leaving clearly discernible vestiges. Add to this the fact that fusion of branches has actually been observed in maize and it becomes apparent that the possibility of fusion in the development of the maize ear cannot be dogmatically dismissed. Nevertheless the fusion hypothesis, in spite of the new evidence which may appear to support it, remains scarcely more satisfactory than it was before.

Hybrids of Guarany Maize and Pod Corn

The real nature of the ear of maize, at least of one type

of ear, is strikingly revealed by ears from a cross of pod corn (tunicate maize) with a variety of maize obtained from the Guarany Indians of Paraguay. The Guarany maize has many peculiar and interesting characteristics. It is one of the few varieties from the lowlands of South America whose chromosomes are knobless or almost so. It exhibits almost all of the dominant genes known in maize, a condition to be expected in a primitive variety. It has the most slender and most flexible rachis ever encountered in a cultivated variety of maize. Finally, it has the peculiar characteristic, under some conditions, of exhibiting in the ear an indeterminate habit of growth. When this happens the ear protrudes far beyond the husks and the exposed region of the ear becomes greatly elongated to produce a lax and flexible spike. This condition was first encountered in 1941. An attempt made in 1942 to induce it through treatment did not succeed. In 1944 the condition again occurred spontaneously. What the factors are which are involved in its occurrence is not known. Bonnett (3) states that both staminate and pistillate inflorescences in maize are potentially indeterminate. Apparently the potentiality persists for a longer period in the Guarany maize than in ordinary maize and an opportunity is afforded for environment to play a part. It is of some interest in this connection to note that the indeterminate nature of the ears was much more pronounced in a late-planted row which flowered during a period of very favorable weather, than it was in earlier planted rows which came into bloom during a hot dry period.

The stock in which the indeterminate ears occurred in 1944 was one which had been derived from a hybrid of Guarany maize and pod corn which had been twice back-crossed to Guarany and was therefore seven-eighths Guarany in its germplasm. Tunicate and non-tunicate ears

occurred in approximately equal numbers and both were affected by the elongation which had occurred. The effects were much more striking in the tunicate ears and especially so in the ear illustrated in Plate VIII which represents an extreme example of elongation.

A study of this and similar ears reveals the real nature of the ear of maize more clearly than has ever been possible by anatomical studies. It should be pointed out that these ears are not abnormalities in the sense that the normal course of development has gone drastically awry —they are not teratological phenomena. Instead, the normal potentialities of the ear, apparently always present, have been more completely developed than is usually the case. This, in combination with the tunicate condition, has resulted in ears so elongated and stretched out that the individual nodes of the rachis and the arrangement of the spikelets upon them are clearly revealed, as illustrated by Plate IX.* There is apparently no essential difference between the structure of the ear at the base where it was completely enclosed in the husks and at the tip where it was completely free from the pressure and restraint exerted by the husks. There is a gradual transition, not an abrupt change, from one condition to the other.

There are several definite and important conclusions to be drawn from these elongated ears of Guarany pod corn:

Homologies. There is now no doubt, if there was doubt before, that the ear is the homologue of the central

*The use of genetic characters in studying the nature of various structures of maize and its relatives offers important possibilities. The tunicate gene transferred to teosinte by repeated backcrossing furnishes a most convincing demonstration that the shell of the teosinte fruit is composed of a rachis segment and an indurated glume, as it has been described, and that it is the pedicellate spikelet which is aborted.

spike of the tassel. Except that the spikelets are pistillate instead of staminate and that both spikelets are sessile or almost so, the elongated portion of these ears is scarcely distinguishable from the central spike. Furthermore, for some reason (for which mere coincidence is not a satisfying explanation) a number of these ears have basal branches. Such ears correspond, not to the central spike alone, but to the central spike plus a few of the upper lateral branches of the tassel.

Fusion. The evidence against the fusion hypothesis now amounts almost to complete proof at least for this type of ear. The rachis is a simple stem-like structure exhibiting not the slightest evidence of fusion in external morphology or internal anatomy. There is no more reason for suspecting fusion in this rachis than in the rachis of wheat, oats, barley or other cereals.

Phyllotaxy. The phyllotaxy is verticillate or whorled rather than spiral. The ear is a simple spike with the spikelets arranged in whorls at the nodes (Plate IX). The number of pairs of spikelets at each node varies, but it is usually two or three. On one ear, beginning with the first node at the tip, the number of pairs of spikelets was 1, 1, 2, 2.5, 3, 2.5, 3 respectively for the first seven nodes. Thereafter three pairs of spikelets occurred at every node up to the 67th, beyond which it was impossible to distinguish the nodes. In a second ear the number of pairs of spikelets was 2, 2, 2, 2, 2, 2, 2.5 for the first seven nodes; two pairs of spikelets each on nodes eight to twenty-four; three or four pairs of spikelets on all additional nodes.

There is a tendency for the pairs of spikelets at one node to alternate in position on the circumference with those at adjacent nodes above and below. In a region of the ear where two pair of spikelets at each node is the

predominating condition, the result is a decussate arrangement which, since the spikelets are paired, actually appears as a double decussate condition.

Spiral phyllotaxy, when it occurs, seems to be accidental. There are regions of the ear in which the phyllotaxy ostensibly is spiral, but this is apparently the result of crowding, and is not the underlying or basic arrangement. This will become clearer when the number of rows is discussed.

Number of Rows. The number of rows is variable. In the elongated region of the ear the spikelets do not appear to be arranged in definite rows, and the orderly arrangement characteristic of most maize ears is lacking. In the basal portion of the ears, the part covered by husks, the grains are arranged in rows, but the number is not constant. It increases rapidly toward the base. In one case row numbers of eight, ten, twelve and fourteen were counted on a single ear. There is not, however, the definite dropping of a pair of rows at any point, as in the cobs described by Weatherwax (17). At one level of the ear eight rows can be counted, at another (lower) level ten, but it is difficult to determine the points where pairs of rows have terminated.

The number of rows is largely independent of the underlying arrangement of the spikelets. In one ear in which the number of rows increased progressively from eight to ten, and from ten to twelve, the underlying arrangement of the spikelets remained the same, three pairs of spikelets at each node. The fact that there are rows at all seems to be largely the consequence of crowding. The spikelets apparently are forcibly crowded into that arrangement which is the most efficient from the standpoint of utilizing space. Certainly there is no definite underlying structure which results in the orientation

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of the spikelets into clear-cut ranks as in the case of ears of many North American varieties. Straight rows in this case are probably similar to the rows seen in young inflorescences of Pennisetum (Weatherwax, 19).

Pairs of Rows. Lines of demarcation between pairs of rows, commonly seen in ears of North American varieties, usually separate one rank of paired spikelets from the adjoining rank of paired spikelets. In the Guarany maize the lines of demarcation *separate the two spikelets of the same pair* and a pair of rows thus represents spikelets from two adjacent ranks of spikelets intermeshing with each other like the teeth of gears. This is illustrated in Plate X.

Compaction of the Inflorescence. Since the chief, if not the only real, difference between the upper and lower regions of these ears is one of elongation, it follows that one of the important characteristics of the normal ear of maize lies in the fact that it is a strongly compacted inflorescence. In the ears of Guarany pod corn there is a strong correlation between the amount of compaction and other characteristics. As the ear becomes more compacted, the internodes become shorter, the rachis becomes thicker and the *number of rows of grain increases*. These associated changes are illustrated by the three specimens shown in Plate X.

The correlation between condensation of spikelets on the lateral branches of the tassel and the number of rows on the ear which Anderson (1) has reported may represent one manifestation of the relationship between compaction and number of rows. But since the correlation which he observed is characteristic of North American maize and apparently does not hold for South American varieties (1), it is more likely that condensation of spikelets is correlated with the number of spirals of the under-

lying spiral phyllotaxy which, as will be shown later, is characteristic of North American maize.

If these elongated inflorescences of Guarany pod corn are a valid criterion (and there seems to be no good reason to doubt that they are since they do not appear to represent a teratological condition), then the ear of maize is much less complex than has generally been supposed. It is nothing more than a strongly compacted spike in which pairs of spikelets are borne in varying number in whorls at the nodes of a simple non- or weakly-articulated rachis. This description, however, applies only to ears of the general type exemplified by the Guarany variety. A second type of ear apparently exists and is considered below.

Crosses of Maize and Teosinte

The hypothesis, already discussed, of a polystichous ear developing from a distichous spike through shortening and twisting of the axis was based on observations which Collins (5) had made upon segregates from maize-teosinte hybrids. In his paper he showed photographs of spikes representing the various steps assumed to have been involved; the restoration of the aborted spikelet, the yoking of adjacent segments of the rachis, and finally the change from distichy to polystichy. His figures are not too convincing. Especially lacking are specimens showing the transition from independent to yoked rachis segments. Nevertheless his description is correct in its principal details. My own material, probably because I have had much larger populations than Collins to draw from, show the transition from the independent to the yoked condition much more clearly than did his (Plate XI, figs. A, B, C). In teosinte the joints of the rachis stand almost directly above or below one another to produce a structure which Collins has aptly described as

"resembling a string of triangular beads" (Plate XI, fig. A). As the axis shortens or the rachis segments increase in size, the segments tend to lose their linear orientation and to assume a zigzag arrangement (Plate XI, fig. B). Finally adjacent segments, whose spikelets arise on opposite sides of the axis, become diametrically opposed to each other and yoked to each other (Plate XI, fig. C).

The other steps which Collins described also occur regularly and here, too, my material is better for purposes of illustration than was his. The change from solitary to paired spikelets is shown in Plate XI, figs. A and D. This may occur either before or after the rachis segments have become yoked. The change from distichy to polystichy to produce an eight-rowed ear is shown in Plate XI, figs. E and F. Collins attributed this change to a twisting of the axis and the term is satisfactory if it is not used too literally. What actually occurs is that the yoked segments become arrayed in two planes instead of one, an arrangement which makes much more efficient use of the circumference of the rachis as a spikelet-bearing surface. Collins showed diagrammatically how ears with additional row numbers would be produced by additional "twisting" of the axis. These were not encountered in my material. A number of ten-rowed ears occurred, but they were, for the most part, "disharmonious" ears with twisted cobs. Apparently the only "normal" ears in which the yoking is readily discernible are four-rowed and eight-rowed ears.

An important change which Collins did not note, or at any rate did not describe, is the compaction of the inflorescence. A spike which has passed through the three stages which he described is still far removed from an ear of maize. It must pass through still another stage, a change from a lax spike to a compacted spike. Plate XI, fig. G illustrates an eight-rowed spike which has become

compacted and which is recognizable as an ear of maize.

What conclusions can be drawn from this series of transition forms which occurs in maize-teosinte hybrids? Collins was cautious on this point, stating that these intermediate forms are of value primarily in throwing light upon the morphology of the ear and explaining its evolution in a mechanical sense. Weatherwax (18) was even more circumspect in his statement on this subject, which follows: "Hybrids between maize and teosinté will always exhibit suggestive series; but, until we are more sure of the homologies between these two genera, it is futile to expect much information from the hybrids, for they will be speaking in a language that we cannot understand."

Now, when the homologies of maize and teosinte are somewhat better understood than they were two decades and more ago, and when the rôle of genetic mechanisms in evolution has also become much clearer, speculation on the meaning of the hybrid forms may be permitted.

If maize has originated from teosinte under domestication, as some students of the problem have assumed, then hybrids of the two species are capable of revealing something about the nature and extent of the genetic changes which have occurred. If we accept this interpretation we need only to state here that the genetic changes involved have been numerous and far reaching in their effects, and that the period of domestication of maize has either been very long indeed or mutations must have occurred at an unprecedented rate, for maize differs from teosinte by numerous genes distributed among a number of different chromosomes. If on the other hand teosinte is the product of the hybridization of maize and Tripsacum, as postulated by Mangelsdorf and Reeves (13), then hybrids of maize and teosinte simply show the effects which are produced upon maize by various doses

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of Tripsacum germplasm. This becomes especially important in considering the correlative hypothesis of Mangelsdorf and Reeves (13) that new types of maize originating directly or indirectly from the hybridization of maize and Tripsacum comprise the majority of the varieties of Central and North America.

Teosinte (Tripsacum) germplasm consistently has certain definite effects upon the structure of the ear of maize. These effects vary considerably with the amount of teosinte germplasm involved and with the genetic level at which it is operating. In spikes approximately intermediate between those of maize or teosinte (spikes similar to those borne on F_1 plants of maize-teosinte hybrids), small differences in the proportion of maize and teosinte germplasm can mean drastic changes in external morphology, for example: from distichy to polystichy or from single spikelets to paired spikelets. As the segregates approach either end of the range, however, much larger increments are necessary to produce these changes.

These facts, revealed by F_2 segregates of maize-teosinte hybrids, are even better illustrated by stocks in which an entire teosinte chromosome or a part of a chromosome has been transferred to a uniform inbred strain of maize by repeated backcrossing accompanied by selection. Stocks developed in this way are isogenic in nine of their ten chromosomes and therefore approximately identical with the original inbred strain of maize. The remaining chromosome, however, has been substituted for, wholly or in part, by a corresponding chromosome from teosinte.

The substitution of a small amount of teosinte germplasm for maize germplasm at this level has no apparent effect whatever upon such characteristics as paired and single spikelets; the spikelets remain completely paired. But these doses of teosinte germplasm do consistently reduce the number of rows of grain and they consistently

tend to make the cob stiffer and more indurated, and to give the rows of grain a rigid vertical alignment sometimes accompanied by spaces between pairs of rows. The end product of these various tendencies is most commonly an eight-rowed ear in which spikelets in one plane are diametrically opposed to each other, while those in the plane at right angles to the first are also opposed to each other but in positions alternating exactly with those in the first plane.

Here, then, is precisely the kind of ear which would have developed according to Collins' yoking and twisting hypothesis. The only difference is that the rachis having become large, and sometimes pithy, the yoking is no longer actually apparent. But these ears also conform completely to Weatherwax's conception of the ear as an example of spiral phyllotaxy. Indeed the spiral phyllotaxy is so rigid that the addition of another pair of rows of grain, the equivalent of a half-spiral, results in an unbalanced phyllotaxy usually accompanied by a twisting of the cob. This type of ear is obviously quite different from that illustrated by the Guarany pod corn; and yet the one is nothing more than a modified form of the other.

That there are differences in maize varieties with respect to phyllotaxy in the branches of the tassel has already been noted by Anderson (1) who finds a spiral phyllotaxy predominating in some varieties, a whorled phyllotaxy apparently characteristic of others.

Other Differences in Maize Types

If there are in nature two types of ears, one with a whorled phyllotaxy another with a spiral phyllotaxy, it is reasonable to suspect that other differences between the two types also exist.

Arrangement of Spikelets. Another important difference in the two types may lie in the arrangement of the sessile and pediceled spikelets on the ear. If the ear of maize is a spike only recently derived from a panicle by reduction of branches then the arrangement of the paired spikelets with respect to the position of the pediceled and sessile member of each pair should be largely a random one because the branches of the panicle are arranged at random with respect to the position of the pediceled and sessile spikelet of the lowest pair. If, however, the ear has come under the influence of Tripsacum genes to the extent that it behaves as a structure derived from the distichous spike of teosinte, then the arrangement of the spikelets may well be a systematic one.

Unless I have inadvertently overlooked a reference to it in the literature, the question of the arrangement of sessile and pediceled spikelets on the ear seems never to have been answered. Collins (5), assuming that it is always pediceled spikelets which abort when rows of grain are dropped between the base and tip of the ear, asserted that he had never seen an instance where the dropped rows were either adjacent or separated by two rows. This he regarded as evidence that the arrangement of pediceled and sessile spikelets around the circumference of the ear is not the one expected from the fusion of two-ranked spikes. He apparently concluded, although he certainly did not prove, that the arrangement is, instead, the one that would be expected if the ear had resulted from yoking and twisting in the distichous spike.

Actually, since all pistillate spikelets are sessile (although one member of each pair is potentially pediceled) it is impossible to determine from the external appearance of the ear the nature of the arrangement of its spikelets. But since the central spike of the tassel is clearly the homologue of the ear, and since on the central spike the

sessile and pediceled spikelets are often readily distinguished, it should be possible to draw some inferences about spikelet arrangements in the ear by studying them on the central spike.

The spikelets on the central spike of the tassel are borne in more or less distinct rows. These are less clear cut, to be sure, than those on the ear, but can nevertheless be traced with a fair degree of accuracy. The position and arrangement of the spikelets on a central spike can be charted by tracing a vertical rank of spikelets from its base, determining the position of each pair by actual measurement and noting whether the pediceled spikelet is at the right or left of the sessile one. This is repeated with each vertical rank until the entire circumference of the spike has been charted.

A chart of the spikelets of the central spike, prepared in this way, is almost the equivalent of peeling the surface of the rachis, unrolling it and spreading it flat.

Plate XII, figs. D and E, shows in diagrammatic form the relative position and the arrangement of sessile and pediceled spikelets on portions of central spikes of two inbred strains of maize; the first a strain of the Guarany variety; the second a North American strain well known to agronomists, K155.

It is to be noted that in the Guarany maize the arrangement of the spikelets with respect to the position of the sessile and pediceled is a random one, or at least the deviation from randomness on any single row is clearly not significant.

The central spike of K155 presents quite a different aspect. In one row (the center row in the diagram) the spikelets are arranged at random, but in the remaining rows the arrangement is either clearly systematic or it approaches this condition. In the second row from the left, for example, the pediceled spikelet is at the left in

all (seven) pairs. In the fourth row the pediceled spikelet is at the right in all (eight) pairs. A systematic arrangement is also closely approached in the first and fifth rows, the former having the pediceled spikelet at the right in six of the seven pairs, the latter having the pediceled spikelet at the left in eight of the ten pairs.

It is to be noted further that the second and fifth rows in this diagram are mirror images of the first and fourth with respect to the position of the pediceled and sessile spikelets.

How does the arrangement in Fig. E compare with the arrangement theoretically expected if the ear of maize had originated from the spike of teosinte by yoking and twisting? Plate XII, fig. A shows the arrangement in teosinte when the abortive spikelet becomes functional, as it does in some cases, especially when the tunicate gene is superimposed upon teosinte by crossing and backcrossing. Here the arrangement is completely systematic and the two ranks are mirror images of each other with respect to the position of pediceled and sessile spikelets.

Plate XII, fig. B shows the theoretical arrangement after yoking has occurred. This arrangement has actually been seen in a segregate from a maize-teosinte hybrid in which the spikelets were yoked, both spikelets of each pair were functional and the pediceled spikelets were distinguishable from the sessile ones.

Plate XII, fig. C shows the theoretical arrangement resulting from yoking combined with twisting of the axis. Here rows one and three and rows two and four (rows diametrically opposed to each other on a cylindrical rachis) are mirror images of each other with respect to arrangement as well as position of the spikelets.

In two important characteristics, systematic arrangement of the spikelet and mirror imagery, K155 is like the ear theoretically developed from the spike of teosinte

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through yoking and twisting. But in a third important feature, the sequence of pediceled and sessile spikelets, there is a distinct difference. In the ear developed from teosinte by yoking and twisting (Fig. C) the sequence is **PSPSSPSP**. No matter at what point this sequence begins it always involves at some point on the circumference two rows of sessile spikelets adjacent to each other and diametrically opposed on the rachis to two rows of pediceled spikelets adjacent to each other. In K155 (fig. E) on the other hand (omitting the single row with random arrangement and letting the letters S and P respectively, represent the predominating condition in each row of spikelets) the sequence is **SPPSSPPS**. Here no matter on which row the sequence begins, the pattern is one of two rows of sessile spikelets alternating with two rows of pediceled spikelets.

This sequence is not unique to K155. It has been observed in other strains where the arrangement of spikelets approaches the systematic.

The sequence illustrated in Fig. C has also been observed in several varieties. This means, if it means anything at all, that the ear of maize sometimes behaves as though it had been derived from the spike of teosinte by twisting of the axis in the sense in which Collins used the term. Whether this sequence is as common as the other remains to be determined.

Other evidence that both random and systematic arrangement of spikelets occur is found in ears which are partly or wholly staminate at the apex. When wholly staminate both spikelets are usually, though not always, sessile as they are when wholly pistillate. When the spikelets are mixed, however, the pistillate one is usually sessile, the staminate one pediceled. In the Guarany variety the arrangement of staminate and pistillate spikelets, when the two are mixed, seems to be essentially

random. In ears derived from maize-teosinte crosses which have been repeatedly backcrossed to maize, the arrangement is definitely systematic.

The entire subject of spikelet arrangement deserves more study. In the meantime it is already reasonably clear that on the central spike of the tassel, at least, the arrangement approaches a random condition in some varieties and is systematic in others. There is reason to suspect that these differences occur also on the ears. It is supposed that the random arrangement is characteristic of "pure" maize; the systematic of Tripsacum-contaminated maize. Varieties which are completely random or completely systematic in the arrangement of their spikelets are perhaps not common, the majority of varieties probably exhibiting some degree of intermediacy between the two extremes.

Twisted Ears and Odd Numbers of Paired Rows. Attention has been called to Fujita's observation that ears in which the number of rows of paired spikelets is odd are often slightly twisted with the rows of grain exhibiting a tendency to form weak spirals. And mention has also been made of the fact that there is, in North American maize at least, a preponderance of ears with rows of paired spikelets in even numbers as opposed to those with rows in odd numbers. The two phenomena are probably related and both may well be the result of Tripsacum influence. At any rate they are most strikingly displayed in segregates of maize-teosinte hybrids. The predominance of ears with rows of spikelets (in this case single as well as paired spikelets) in even numbers is well illustrated by the following frequency distribution.

Population	Number of Rows of Spikelets				Total
	2	3	4	5	
(Durango Teosinte × Maize) F2	65	45	58	9	177
(Nobogame Teosinte × Maize) F2	86	71	115	27	299

In both crosses there is a decided deficiency of three- and five-ranked ears as opposed to two- and four-ranked ears. Also in both crosses there is a tendency for the three- and five-ranked ears to be twisted. They are obviously the result of a structural unbalance or asymmetry which induces stresses with visible effects.

These phenomena, so conspicuous in maize-teosinte hybrids, are also readily discernible in maize. There are several explanations for them:

1. Reeves (15) suggests that there is a preponderance of ears with rows of spikelets in even numbers because the basic unit of the ear is a *pair* of rows of spikelets rather than a single row. Thus an eight-rowed ear is much more likely to become a twelve-rowed ear than it is to change to a ten-rowed ear. He regards these units as hereditary and in a broad sense they undoubtedly are. It seems more probable, however, that the unit, a pair of rows of spikelets, is a developmental rather than an hereditary one for it is not uncommon in maize-teosinte hybrids to find two-ranked and four-ranked spikes on the same plant. This is not to say that the number of ranks is independent of heredity. There is abundant evidence that the contrary is true. But apparently the genes do little more than determine in a general way whether the spike is to be few-ranked or many-ranked, while developmental factors determine the size of the units by which the differences are to be attained.

2. Any ear strongly influenced by Tripsacum is likely to exhibit a spiral phyllotaxy so rigid that only those combinations which involve complete spirals will be balanced and symmetrical and hence are more likely to occur than those involving fractional spirals. This is perhaps no more than another way of saying that spiral phyllotaxy explains and accounts for the fact mentioned

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above: that the unit of development is a pair of rows of spikelets.

3. Reeves (15) has also pointed out that with a spiral phyllotaxy the rachis segments are probably hexagonal, fitting together "like the engaged teeth of mechanical gears." With an odd number of rows of paired spikelets there is a physical necessity for some kind of distortion. Either the rachis segments must change shape or the ear must become twisted.

The net result of these various factors, which are closely related to each other, is that there is a strong tendency for rows of spikelets to occur in even numbers. When they do occur in odd numbers there is a strong tendency for the ear to be twisted. Stated in still another way; there is a strong tendency for ears of maize to be balanced and symmetrical, rather than unbalanced and asymmetrical

The above discussion applies especially to ears with a rigid spiral phyllotaxy and indurated tissues, the kind of ear derived from maize-teosinte crosses and the kind presumably resulting in nature from Tripsacum contamination. What of "pure" maize, with its whorled phyllotaxy and random arrangement of spikelets, with respect to these phenomena? Many varieties of Bolivian and Peruvian maize, both prehistoric and modern, have rows of grain more strongly spiral than those of the twisted ears of North American varieties. Extreme forms, as Anderson (unpublished) has noted, have "spiral cross-rowing in two directions, like a pine cone." But this condition in Bolivian and Peruvian maize does not give the impression of abnormality. Like the pine cone with which it has been compared, it appears to be perfectly normal. Furthermore the occurrence of spiral rows in Bolivian and Peruvian maize is usually independent of row number. Ears with pairs of rows in even numbers are

no less subject to the occurrence of spiral rows than ears with pairs in odd number.

Finally, in varieties of this kind there is not the preponderance of ears whose rows of paired spikelets are in even numbers, so commonly found in North American varieties. Ears with ten, fourteen and eighteen rows are as frequent as ears with eight, twelve and sixteen rows. This, like the presence of spiral cross-rows, is characteristic of both prehistoric and modern varieties as is shown by the following frequency distribution, which includes modern ears from Isla del Sol in Lake Titicaca and prehistoric ears excavated by Dr. Julio Tello from the Paracas Necropolis in Peru and by Dr. Junius Bird from Arica, Chile. Data on row numbers in the last named collections were kindly furnished by Dr. Edgar Ander-

Collection	Number of Rows of Grain							Total
	10	12	14	16	18	20	22	
Isla del Sol, Bolivia	5	12	19	9	5			50
Paracas, Peru (Prehistoric)		4	10	5	2	2	1	24
Arica, Chile "	1	14	24	10	2			51

son. The situation is the same in all three cases; there is no deficiency of ears in which the number of pairs of rows is odd, indeed the modal number in all cases is fourteen.

DISCUSSION AND CONCLUSIONS

The conclusion that there are two morphologically distinct types of maize ears is not new. Mangelsdorf and Reeves (13) have previously suggested that the maize varieties of America comprise two more or less distinct groups: (1) "pure" maize which traces its descent directly from the original wild corn; (2) Tripsacum-contaminated maize resulting directly or indirectly from the hybridization of maize and Tripsacum. It was assumed that the differences between these two groups were reflected in

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the ears, but no attempt was made to distinguish them on the basis of differences in their basic structures beyond pointing out that many of the Andean varieties (presumably "pure" maize) are characterized by irregular rows of grain, while many Central and North American varieties (presumably contaminated by Tripsacum) exhibit straight rows frequently separated in pairs. Extreme types approaching these descriptions were found by Mangelsdorf and Cameron (12) in a study of maize varieties of western Guatemala and are illustrated in their paper.

Now the evidence that there are two kinds of maize ears basically different in origin, structure and phyllotaxy, if not conclusive, is at least highly convincing.

The first type of ear which is characteristic of the Guarany pod corn and is probably typical of "pure" maize may be described as a compacted spike with pairs of pistillate spikelets borne in varying numbers at the nodes of a simple, weakly articulate rachis. The ear has a whorled phyllotaxy but may assume, more or less fortuitously, especially if the rows and kernels are crowded, the aspect of spiral phyllotaxy. The rows may be straight, especially if the row number is low; but straight rows like spiral phyllotaxy seem to be, as they are in certain other grass spikes, fortuitous rather than the reflection of a particular kind of underlying structure. Straight rows, in some cases at least, seem to represent nothing more than an efficient arrangement assumed upon crowding. Pairs of rows are not distinctly separated and if there is sometimes an apparent line of demarcation between pairs of rows it separates the two spikelets of the same pair and not two pairs of spikelets. The number of rows is a reflection of the degree of compaction rather than of the complexity of the phyllotaxy for the number of rows can change decidedly from base to tip without any change in the underlying phyllotaxy. With respect

to the position of the sessile and potentially pedicellate spikelets, the arrangement of spikelets on the ear is random or nearly so. The tissues of the rachis and glumes are not strongly indurated. There is no tendency, as in many North American varieties, for ears with pairs of rows in odd numbers, ten, fourteen, eighteen, etc., to be in the minority or for such ears to be twisted.

This type of ear is fundamentally identical with the spikes of certain other species of grasses and like many of them is probably derived from a panicle as the result of reduction of branches. There is not the slightest evidence of fusion. There is abundant evidence, however, that the ear is derived from a panicle for the central spike of the tassel, which is unquestionably the homologue of the ear, is still surrounded with basal branches. Indeed the tassel is a perfect example of a combination of panicle and spike and illustrates splendidly the transition from one to the other. The change from panicle to spike is obviously relatively recent, but whether it is the product of domestication, wholly or in part, there is at present no way of determining. The fact that the Guarany variety, which is primitive in certain other characteristics, frequently exhibits basal branching of the ear, suggests, though it does not prove, that the wild maize with which domestication began was at least moderately branched in its lateral (probably pistillate) inflorescences.

This type of ear, it may be said again, differs in no single important characteristic from the inflorescences of other grasses. True, it usually is wholly pistillate, but there are other grass inflorescences, such as the pistillate forms of the dioecious species of *Monantochloë, Jouvea, Buchloë* and *Eragrostis*, which are entirely pistillate. It usually has a massive rachis and large caryopses, but there are varieties of sorghum which have the rachis thicker than the most slender maize cob and the cary-

opses larger than the smallest maize kernels. This ear of maize seems not to possess a single characteristic in which it is consistently unique. Its uniqueness lies rather in the particular combination of characters which it possesses. The fact that it is wholly pistillate, bears large caryopses on a massive rachis and is a strongly compacted inflorescence, readily distinguishes it from all other grass inflorescences.

Of these characteristics the last, compaction, is by no means the least important. Once this fact is recognized —that the ear of maize is one of the most strongly compacted of all inflorescences—then much of the mystery which has surrounded the ear disappears and it becomes scarcely more difficult to understand than a head of cabbage which also is a strongly compacted but otherwise relatively simple structure.

The second type of maize ear, the type which presumably results from Tripsacum-contamination is, like the first, a compact spike. It differs from "pure" maize primarily in having a spiral rather than a whorled phyllotaxy and a systematic rather than a random arrangement of sessile and pedicellate spikelets. Indeed a brief description would appropriately term the first "whorled-random"; the second "spiral-systematic." But there are other differences as well. The tissues of the rachis and glumes of the spiral-systematic type are usually indurated; the rachis as a whole being quite tough, though evidence of an inherent rachis fragility is sometimes discernible. The rows of grain are distinct and not infrequently separated in pairs. When this occurs a pair of rows is the equivalent of a row of paired spikelets. The tendency for a rigid vertical alignment of the spikelets is so strong, probably as the result of an inflexible spiral phyllotaxy, that ears in which the number of pairs of rows is odd are in the minority and are usually twisted.

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The spiral-systematic ear, like its putative precursor the whorled-random ear, furnishes no evidence whatever of fusion. It does, however, have the aspect of a fusion product and especially is this true of eight-rowed ears in which the pairs of rows are distinctly separated with shallow clefts or apparent lines of fissure in the cob corresponding to the lines of demarcation. Furthermore the sequence of sessile and pedicellate spikelets around the circumference, SSPPSSPP, sometimes encountered, is the kind of sequence which would be expected as the result of fusion of two-ranked branches. Nevertheless there is neither evidence of fusion nor necessity for assuming that it has occurred.

There is perhaps no single characteristic by which these two types of maize ears can always be distinguished from each other. Actually pure forms of either are probably rare and intermediate forms are more common than the basic types. There are, however, several circumstances usually associated with the two general types. The "pure" maize with its derivatives is the predominating type in the Andean region of Peru, Bolivia and Ecuador and in the adjoining lowlands of South America, particularly in Paraguay. It is also the predominating type in the prehistoric maize of South America. The same or a similar ear is found at high altitudes in Guatemala and, also at high altitudes, in some localities in Mexico.

The Tripsacum-contaminated maize is typical of most of North and Central America and of most of the lowlands of South America.

It is realized that there is still no actual proof for the existence of "pure" and Tripsacum-contaminated maize. Nevertheless it is now reasonably certain that there are two basically different types of maize ears with more or less distinct patterns of geographical distribution. Since

there is complete interfertility in maize varieties from all parts of America, it is logical to conclude that the one has been derived from the other. Segregates from maize-teosinte crosses and isogenic stocks developed by repeated backcrossing of such crosses to inbred strains of maize demonstrate that teosinte genes can produce the changes by which the two types are distinguished. All of these facts indicate, though they obviously do not prove, that a pure maize originating in South America and bearing ears characterized by whorled phyllotaxy and random arrangement of sessile and pedicellate spikelets has become modified by the introduction of Tripsacum (teosinte) germplasm to produce an ear characterized by spiral phyllotaxy and systematic arrangement of spikelets.

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EXPLANATION OF THE ILLUSTRATIONS

Plate VII. Reproduction of a page of Lyte's (1619) *New Herbal*, which describes the inflorescences of maize.

Plate VIII. Example of extreme elongation in an ear of Guarany pod corn. The lower half of this ear was enclosed by the husk and is compacted with the kernels arranged in rows. The upper half was free of the husks and is intensely elongated.

Plate IX. The basic structure of the maize ear is illustrated by this enlarged ($\times 1.5$) photograph of the elongated terminal portion of an ear of Guarany pod corn. A pair of spikelets has been removed at each node to show the simple rachis bearing spikelets in whorls at the nodes.

Plate X. Relation between compactness and number of rows. The left ear has eight rows at the tip; fourteen rows at the base. The center ear and the naked rachis at right show how the internodes become progressively shorter toward the base. The number of spikelets at each node remains approximately the same.

PLATE XI. Transitions from teosinte to maize illustrated by the pistillate spikes of F2 segregates of a maize-teosinte hybrid. A. Most teosinte-like spike with single spikelets alternating in two ranks. B, C. Transition from independent to yoked rachis segments. D. Approximately like A, except that spikelets are paired. E. Yoked rachis segments combined with paired spikelets to produce a distichous, four-rowed spike, bearing four spikelets at each joint of the rachis. F. Portion of spike and single rachis joint of an eight-rowed spike derived from a four-rowed spike by ''twisting'' of the axis. G. Most maize-like spike. It differs from F primarily in degree of compaction.

PLATE XII. The arrangement of sessile and pedicellate spikelets around the circumference of various spikes. A. Teosinte spike. B. Teosinte spike with yoking of rachis segments. C. Theoretical arrangement resulting from yoking combined with twisting of the axis. D. Actual arrangement of spikelets on a portion of the central spike of the tassel of an inbred strain of Guarany maize. Note that arrangement is random or nearly so. E. Actual arrangement on a portion of the central spike of North American inbred K155. Note that arrangement is strongly systematic.